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Early Development of Continental Ecosystems

Introduction

The fossil record demonstrates a radical change in the character of life in brackish, freshwater, and terrestrial habitats — categorized inclusively as *continental habitats* — in an 80-million-year interval from the Ordovician to the end of the Devonian. This "mega-event" involved not only the origin and diversification of several classes and even phyla of organisms but also extensive changes in the structure and dynamics of continental ecosystems. The most significant of these changes, which first appear in brackish water and extend progressively into fresh water and, finally, terrestrial (nonaquatic) ecosystems, include (1) elaboration and differentiation of trophic structure, (2) increases in productivity, and (3) shifts in dominant ecologic strategies (from resource conservation and mortality replacement to resource aquisition and competition).

Although many workers have speculated on the origin and early evolution of particular groups of nonaquatic organisms, little attention has been given to the development of freshwater or brackish-water ecosystems, and not much more to the structure and dynamics of early terrestrial ones. Olson's work (1966) on the trophic aspects of Permian freshwater and terrestrial communities suggests a starting point for such an analysis. Rolfe (1980) has briefly considered the development of trophic structure in Siluro-Devonian terrestrial communities; Hughes and Smart (1957) and Smart and Hughes (1972) as well as Kevan, Chaloner, and Savile (1975) have investigated coevolution of early terrestrial arthropods and vascular plants; Edwards (1980) and Niklas, Tiffney, and Knoll (1980) have dealt with various aspects of the development of plant communities and adaptive patterns in early vascular plants. Denison's analysis (1956) of habitats occupied by early fish and Størmer's studies (1976) of early continental arthropods have provided important insights into the occurrence and composition of early continental ecosystems. In addition, considerable information can be extracted from the literature dealing with individual fossil taxa and particular floras and faunas and from published interpretations of coeval continental sedimentary rocks.

This chapter opens with a summary of our knowledge of early continental ecosystems and their structure, dynamics, and development. This synopsis will serve to substantiate the explanations of ecosystem development and of evolutionary events and trends that I put forward in the concluding section.

Pre-Silurian Continental Ecosystems

Assemblages and Biocoenoses

The pre-Silurian fossil record of continental biocoenoses is extremely sparse in spite of the widespread occurrence of sedimentary rocks representing continental habitats. Some fossil plant materials reported from late Ordovician near-shore deposits may represent emergent hydrophytes if not fully terrestrial plants (Gray and Boucot, 1977, 1978; Gray, Massa, and Boucot, 1982). Since their remains are known only from transported materials, definite assignment to a more specific habitat — littoral marine, brackish, freshwater, or terrestrial — is not possible. Thorough study of some marginal marine and estuarine deposits of mid-Ordovician age failed to yield macrophyte traces (Spjeldnaes, 1979; Fischer, 1978) and studies of Ordovician paleosols, although so far quite limited, argue against the presence of vascular plants or even of large, erect nonvascular ones in terrestrial habitats though they do not preclude the presence of microphytes or sprawling nonvascular macrophytes (Retallack, n.d.). Further, Cotter (1978) argues that the rarity of sinuous stream deposits in pre-Silurian continental sediments demonstrates the absence of rooted macrophytes, and Basu (1981) reaches a similar conclusion from the relatively great abundance of unweathered detrital potassium feldspar in these rocks (see below). The presence of a continental microflora, however, is indicated by the occurrence of stromatolites in deposits interpreted as brackish and freshwater (Hoffman, 1976; Hofmann, Pearson, and

Wilson, 1980) and by the similarity of some late Proterozoic microbial fossils to modern, subaerial prokaryotes (Golubic and Campbell, 1979). One may reasonably infer the presence of blue green and green algae and, in terrestrial habitats, lichens.

Evidence of continental faunas is equally sparse. Possible brackish-water deposits of mid-Ordovician age in Colorado yield medium-sized agnathan fish and medium- to large-sized arthropods (scorpions, eumalacostracans, aglaspids, synxiphosurans, and limulines — but, very strikingly, no euripterids) (Fischer, 1978). Spjeldnaes (1979) suggests that some Ordovician assemblages of agnathan fish and lingulid brachiopods were exposed to variable salinity. In addition, by analogy with similar occurrences in younger rocks, one might expect that some of the low-diversity, bivalve-lingulid assemblages in middle and late Ordovician deposits also represent brackish habitats. Finally, some shallow-water, near-shore trail-and-burrows assemblages ("Skolithos" and even "Cruziana" ichnofacies) may represent brackish-water biocoenoses (Fischer, 1978). Even if all these Ordovician assemblages are truly brackish-water, the abundance and diversity of the macrofauna, however, was clearly much lower in them than in comparable Siluro-Devonian assemblages (see below). The Ordovician brackish-water assemblages are not as clearly differentiated in taxonomic composition from marine assemblages as those in younger deposits.

At present, knowledge of freshwater and terrestrial animals is limited to burrows observed by Retallack (1981) in some late Ordovician paleosols. He attributes these to small arthropods, but the interpretation is not definite. One might reasonably expect the presence of such organisms as part of a soil microbiota; such organisms are very rarely fossilized, and their absence as body fossils is to be expected. Although early fish and euripterids have been interpreted as members of early freshwater ecosystems (Romer, 1955), all pre-Silurian (and most Silurian) fish occur in what appear to be marine or brackish-water assemblages (Denison, 1956; Spjeldnaes, 1979; Boucot and Janis, 1983). Further, Ordovician euripterids typically occur in marine or even hypersaline assemblages (Caster and Kjellesvig-Waering, 1964) and do not appear in brackish-water and freshwater ones until middle and late Silurian.

Habitats

Prior to the extensive deployment of macrophytes, continental habitats must have been very different from modern equivalents with respect to resources, physical disturbance, and uncertainty (that is, spatial patchiness and temporal instability). At present, macrophytes, particularly the tracheophytes, strongly influence the weathering and hydrologic regimes in continental environments and thus the patterns of erosion and deposition as well as the storage of water and release of mineralized nutrients. They not only control microclimates but also affect macroclimates. Finally, they are the dominant food sources for secondary production in most aquatic as well as terrestrial habitats.

The most important environmental effect of macrophytes involves differences in weathering rates and processes. First, the rate of chemical weathering would have been considerably lower without a cover of rooted (or rhizoid-bearing) plants because of (1) the low partial pressure of CO_2 in soil water due to a relative paucity of organic detritus, (2) the low level of fungal leaching due to the absence of root mycorrhiza and the paucity of detritus, and (3) the paucity of moisture resulting from rapid throughflow of soil water (see below). Moreover, the absence of deep root zones would have limited biologically mediated weathering to a near-surface film. Cawley, Burruss, and Holland (1969) found the rate of chemical weathering in central Iceland to be two or three times greater in areas covered by vascular plants than in those limited to lichens and bare soil. Basu (1981) presents evidence for low rates of weathering of potassium feldspar in the absence of plants, presumably due to the lack of direct uptake of potassium by plant roots. The same chemical situation would presumably hold for other critical nutrient ions, for example, phosphate, that are taken up selectively. It seems likely, therefore, that the overall release of nutrient ions from pre-Silurian, terrestrial soils was one-half or less than that at present (and much less if lichens were absent). This shortage would have limited productivity in continental habitats and affected nutrient availability in freshwater and marine systems.

Second, the physical character of soils probably differed on the average from modern ones. In particular, a lower rate of chemical weathering probably resulted in a lower production of clay minerals and a relative dominance of silt over clay in the fine fraction. Such a comparative shortage of fines would have been exaggerated by relatively high rates of splash and sheet erosion and of eolian deflation on unvegetated surfaces (except as opposed by algal and lichen crusts). Wind erosion would also have been intensified because of relatively high velocities close to the ground in the absence of plant windbreaks. Overall, the result of the absence of macrophytes would have been a relative predominance of sandy and rocky soils of high permeability but low porosity. Such soils would have had high infiltration capacity but low water retention, transforming surface runoff to rapid throughflow in the soil zone. Fine-grained, water- and nutrient-retentive soils would have been limited largely to lowland, alluvial or lacustrine areas.

The existence of such a physical regime would have had serious consequences for terrestrial plants. Essential ions for plant nutrition, held in modern soils on clay and organic aggregates, would have been removed very rapidly because of low retentivity and high water flux; only a small amount could have been retained in the algal or lichen crusts. Further, the upper soil zone would be quite dry except during and immediately after rainfall. Unvegetated soils would have dried rapidly, and surface moisture would have been quite unpredictable. Temperature variations would also have been very large.

The hydrology of terrestrial drainage basins would have differed because of a higher proportion of runoff and throughflow to interception and transpiration. Schumm (1968) suggests that in such circumstances the mean annual runoff would be 100 percent greater for a given annual precipitation than that observed in modern continental habitats. High, "flash" discharge implies a high rate of erosion aggravated by the absence of roots to check water flow and bind small particles, although algal crusts would reduce erosion somewhat. Such rapid erosion would have tended to maintain thin, rocky soils with very low storage capacity for either water or dissolved nutrients.

The physical and chemical characteristics of the streams would have reflected the differences in weathering, soils, discharge, and erosion. For a given climatic regime, stream water would have displayed relatively low ion concentrations (because of lower rates of chemical weathering and higher rates of discharge). Fine sediment trapped in the pools would have carried fewer absorbed ions because of the lower organic content (and, possibly, a lower clay fraction). Less fine sediment would be trapped because of the absence of aquatic macrophyte "baffles." Nutrient ions, rather than being accumulated by macrophytes and plant detritus and held for slow release and recycling, would have been lost rapidly. Finally, such nutrients as might be held in alluvial sediments would remain entombed rather than being pumped back into the ecosystem through the root systems of aquatic macrophytes (see Moss, 1980, 141, on the role of rooted macrophytes in modern freshwater ecosystems). Oxygen partial pressures in the water would vary primarily with temperature, since organic decomposition would consume relatively little oxygen; conversely, decomposition would tend to be rapid and thorough. Carbon dioxide partial pressures would tend to be far below saturation for the same reasons. The "flashy" hydrologic regimes would produce severe floods of quite brief duration, interspersed with periods of extremely low flow confined to channel thalwegs; stream waters would be very turbid and have a heavy traction load. These characteristics, together with highly variable discharge and lack of rooted bank vegetation would favor development of braided streams (Schumm, 1968). Channels and bars both would be subject to rapid change and be of impermanent character. (Cotter, as noted above, reports the predominance of braided, and rarity of sinuous, stream deposits in pre-Silurian sedimentary rocks.)

Lakes would also have diverged in character, although to a lesser extent than streams diverged, because of the differences of input associated with such extremes in weathering, erosion, and runoff as well as because of the absence of macrophytes. The lower input of dissolved nutrients in stream flow and the loosely bound nature of nutrients in sediments would have limited microphyte production. Additionally, the absence of macrophytes would have reduced nutrient accumulation in the ecosystem and, even more significant, reduced recycling from lake-bottom sediments. Thus oligotrophic lakes would have been proportionally much more abundant than at present, although some lakes presumably could have accumulated dissolved nutrients, given favorable local input/output ratios (at the cost, however, of being extremely alkaline and thus unfavorable for most organisms). Flood-basin lakes would have been relatively turbid, nutrient-poor, and subject to extreme changes in level and to extended periods of desiccation. Early lacustrine stromatolites such as the Proterozoic ones described by Hoffman (1976, 609–11) seem to represent such circumstances. Shallow, ephemeral ponds and backwater lagoons would have existed in the place of swamps and marshes; these might be enriched through accumulation of algal detritus, but would have been dried mudflats most of the year. In the absence of a leaf canopy, their temperatures would have fluctuated violently.

Estuaries and lagoons would have shown features similar to those of the lakes but with some further moderation due to the influence of ocean water. Input of dissolved nutrients and their accumulation and recycling in organic detritus would have averaged considerably below the modern rate. Even though seawater influx would tend to ameliorate such shortages (see Hopkinson and Day, 1979, and Fisher, Carlson, and Barber, 1982, on marine-continental balances in modern coastal ecosystems), there could have been no local recycling from buried sediments in the absence of rooted hydrophytes. One might also expect more marked variation in salinity as a result of the extreme variation in river flow — that is, brief episodes of extreme dilution alternating with periods of normal salinity (see Livingston and Duncan, 1979, on the effect of clear-cutting on modern estuaries and lagoons). Sediment transport, erosion, and deposition would also have differed because of the absence of macrophyte baffling and sediment binding in the littoral zone and because of the marked variation in sediment influx from the continent (marked, short-term alteration between high constructional and high destructional regimes).

Global environmental variables (atmospheric composition, ionizing radiation, paleogeography, and climatic zonation) do not appear to have exerted an unusual influence on early Paleozoic continental habitats or ecosystems. Carbon dioxide and oxygen partial pressures in the atmosphere are apparently regulated by biotic and chemical processes within the ocean (Garrels, Lerman, and Mackenzie, 1976; Walker, 1977). The near-constant distribution of marine communities since the late Cambrian argues for a partial pressure of oxygen much like that of the present, certainly within one order of magnitude (Rhoads and Morse, 1970; although Chapman takes an alternative view in this volume). If the oxygen partial pressure were more than 1 percent of the present level, then the flux of ultraviolet (UV) radiation could not have been significantly greater than at the present (Ratner and Walker, 1972); the presence of very shallow water marine communities in pre-Silurian sediments argues against high-intensity UV radiation at the ocean's surface.

Influence by paleogeographic factors is equally obscure. The distribution of particular continental units changed radically through the early and middle Paleozoic (Ziegler, Scotese, et al., 1979), but these changes probably had little effect on the nature and/or abundance of various continental habitats and thus did not direct phyletic evolution or ecosystem development. Even though one might postulate that geographic changes affected rates of species origination and extinction and produced unique ecologic interactions among previously isolated species, such effects would not seem *a priori* to demand any particular direction. (If, however, the development of continental ecosystems depended on extremely rare evolutionary events, the rate of speciation and the frequency of unique ecologic events during any particular interval would affect the likelihood of such events.)

Climatic indicators suggest polar as well as subtropical and tropical climatic regimes (Drewry, Ramsey, and Smith, 1974). The location of the zonal boundaries may have differed somewhat from the present due to differences in continental albedo and evaporation (plus transpiration) (Ziegler, Bambach, et al., 1981). On a global basis these differences would presumably reduce the importation of moisture into the subtropical zone from the adjacent equatorial and high-latitude belts and widen the subtropical arid/semiarid climatic belts (Charney, Stone, and

Quirk, 1975). This situation would increase the continental area subject to extreme uncertainty in rainfall and would have yielded a climatic pattern consistent with the occurrence of red beds at atypically low and high latitudes during this interval. In the absence of terrestrial macrophytes, rainfall patterns may also have differed from present patterns. Plant transpiration is a major factor in recycling water.

Extensive development of continental ice sheets in polar Gondwanaland during the late Ordovician must have been correlated with relatively major climatic fluctuations and episodic changes in sea level. The climatic variation was presumably similar to that in the Pleistocene (Ziegler, Bambach, et al., 1981, 234) and thus would have involved some latitudinal shifts in the boundaries of climatic zones and some expansion of the area of wet-dry and dry habitats. Whether sea-level changes (McKerrow, 1979) had any significant effect other than geographic displacement of coastal and lowland alluvial habitats is not clear, but theoretically eustatic regression might expose more of the gently sloping continental shelves and thus expand the area of such habitats. Pratt, Phillips, and Dennison (1978, 144–45) attribute late Ordovician–early Silurian alluviodeltaic deposits in the Appalachians to such an event. An increase in the extent of coastal lowland areas, if it occurred, might have increased the number of such relatively rich, favorable, and stable continental margin habitats. Such a development would have strong potential effects on both ecosystem development and organismal evolution (Gray and Boucot, 1978). On the other hand, paleogeographic reconstructions for the Cambrian and Ordovician show extensive lowland areas over most of the continental interiors (for example, Scotese et al., 1979), so there would have been no scarcity of such habitats in the early Paleozoic.

Overall, as noted by numerous authors (Swain and Cooper-Driver, 1981; Gray and Boucot, 1977), pre-Silurian continental habitats were marked by limited resources of inorganic nutrients and water, by severe physical stresses that would have interfered with resource utilization, and by extreme physical patchiness and temporal instability. Deductively, one would expect these constraints to be most severe in terrestrial habitats, particularly in continental interiors and uplands, and least severe in large, permanent delta lakes, brackish lagoons, and estuaries.

Ecosystems

With such limited evidence from fossils and rocks, the reconstruction of pre-Silurian ecosystems primarily depends on deduction from modern analogues and from general ecologic principles. The scarcity of fossils suggests that most or all of the organisms were small and that any large ones lacked lignified or mineralized structure and/or were extremely rare. One can also exclude groups whose evolutionary origins are known to be post-Ordovician. Finally, the habitat characteristics (inferred from the absence, or near absence, of macrophytes and from the sedimentologic evidence) set limits on ecosystem structure and dynamics as well as on individual adaptions.

In terrestrial habitats, the limited availability of water as well as slow release and low retention of inorganic nutrients would have kept primary productivity to a very low level except in the most favored sites. High physical stress and uncertainty would have further limited production to brief time intervals in small, scattered sites. The primary producers were predominantly microphytes, with macrophytes contributing very little, if anything. Secondary production in the micro- and meiofauna must also have been limited in amount and in temporal and spatial distribution. These faunas presumably included a mixture of microherbivores and decomposers (representing a second trophic level) plus meiodetritivores and meiopredators (the third trophic level) not unlike those in modern dry-soil biotas (Rolfe, 1980; the burrows reported by Retallack, 1984, may represent such organisms). The lack of fossils representing a macrofauna suggests the absence, or at least the extreme rarity, of animals at the fourth trophic level (except parasites). The typical structure of these early terrestrial ecosystems would thus have comprised three trophic levels with a decomposer loop.

Freshwater ecosystems would also have differed from modern analogues, though perhaps less sharply than did the terrestrial ones. In general, stream ecosystems would have been subject to severe disturbance with unpredictable variation in discharge and with episodic, rapid erosion and deposition. At present, such ecosystems are highly dependent on allochthonous organic matter and on autochthonous production by rooted, semiaquatic macrophytes (Moss, 1980; Welcomme, 1979). Neither planktonic nor benthic microphytes contribute much to the food base except where eutrophication is extreme or where they accumulate in the semiponded, lower reaches of large streams (Roberts, 1972). With very low release of dissolved nutrients from the land by weathering, and without nutrient retention and recycling by rooted plants, microphyte productivity would have been even lower in pre-Silurian ecosystems than in modern analogues. One may reasonably assume (as discussed above) the presence of decomposers and a fauna of small animals including micro- and meioherbivores, meiodetritivores, and meiopredators. Again the lack of macrofossils suggests that consumers representing the fourth trophic level were absent, though one cannot rule out some opportunistic macropredators, for example, large arthropods, invading from brackish habitats. Pre-Silurian aquatic ecosystems are further differentiated from later ones by the absence of the macrodetritivores, for example, some arthropods as well as agnathan fish, which are known from Ordovician brackish-water deposits as well as from middle Silurian and younger alluvial ones.

Autochthonous primary production in lacustrine habitats would also have been restricted by low input of both dissolved and organically bound inorganic nutrients and by the lack of rooted plants to recycle such nutrients after burial in bottom sediments. While input of allochthonous organic detritus would have been relatively small, lakes should have been more productive on the average than rivers and supported at least moderate algal productivity and standing crop. Physical conditions, though fluctuating more than those in modern equivalents, would still have been more stable than in coeval stream or terrestrial habitats. Here again the presence of micro- and meiofaunas at three trophic levels may be presumed, but the lack of macrofossils suggests the complete absence of a fourth trophic level and of macrodetritivores.

The latter situation may, however, be more apparent than real; Ordovician lacustrine habitats are inadequately sampled because of (1) relatively limited investigation of pre-Silurian continental deposits; (2) dominance of piedmont plain, braided-stream deposits in some of the more thoroughly studied units — for example, the Juniata Sandstone of the central Appalachians (Cotter, 1978) — a regime not likely to include either permanent flood-basin or deep-basin lakes; (3) rarity of large animals in unproductive habitats; and (4) the difficulty in finding pre-Silurian fish fossils, which consist almost entirely of small, obscure, isolated tubercles or spines (Spjeldnaes, 1979). Thus, although Denison (1956) has argued persuasively for a marine origin for the vertebrates and for the marine origin of pre-Ludlovian fish, his evidence and interpretations are not incompatible with a limited penetration of fish into delta-plain lacustrine habitats during the Ordovician. Certainly the classic occurrences of fish in the Harding Sandstone appear to include sites representing at least brackish-water habitats.

Brackish lagoons and the estuarine portions of large, sluggish rivers would have resembled large lakes except for (1) the potential addition of dissolved nutrients through seawater mixing and (2) the disturbance associated with tides and oceanic storms (Fisher, Carlson, and Barber, 1982). In many modern analogues, rooted macrophytes (for example, mangroves or salt grass) are the dominant producers and also enhance microphyte productivity by recycling mineralized nutrients locked in bottom sediments. Without rooted macrophytes, the principal production would presumably be in the marine-dominated portions of these habitats. Some Ordovician faunal assemblages (Spjeldnaes, 1979) appear to record habitats that had near-normal salinity much of the time and therefore were subject to frequent colonization by marine organisms.

The only strictly brackish-water ecosystem known from the Ordovician seems to be that reported by Fischer (1978) from a few localities in the Harding Sandstone in Caloradic, which have yielded a rather small number of fossils. Trophic structure of the ecosystems represented by these occurrences is obscure, but the absence of any macrophyte traces suggests the predominance of microphytes as producers; the fish and some of the arthropods were probably deposit feeders (detritivores), and the lingulids were suspension feeders. Some of the arthropods may have been macropredators, but since they preyed primarily on the large deposit feeders (effectively at the second tropic level), they may be regarded as representing the third rather than fourth trophic level. In any case, the deposit feeders appear to show much greater variety than suspension feeders and predators. Though a single occurrence can hardly support very precise conclusions about average conditions, the general Ordovician situation contrasts markedly with that in the Devonian, where "upper-estuarine" assemblages are common, definitely include a fourth tropic level, and produce relatively large numbers of individuals (see discussion below). On the other hand, the occurrence of several groups of arthropods as well as fish in brackish habitats demonstrates that these forms had already adapted to low-salinity environments and that the paucity of such occurrences in the Ordovician (and early Silurian) cannot be attributed to tardiness in evolution of osmoregulatory capacities. This suggests in turn that the absence of arthropods and fish from Ordovician and early Silurian freshwater biocoenoses results from some environmental constraint other than low salinity.

Siluro-Devonian Assemblages, Habitats, and Ecosystems

Overview

The number and the distinctiveness of continental assemblages increased through the Silurian and Devonian. This sequence resolves, at least in Europe and North America, into four phases:

1. Llandoverian and Wenlockian Ages (early and middle Silurian, approximately 445–430 million years before the present);

2. Ludlovian and Pridolian (middle and late Silurian, 430–415 m.y.b.p.);
3. Gedinnian, Siegenian, and Emsian (early Devonian, 415–395 m.y.b.p.);
4. Eifelian, Givetian, Frasnian, and Famennian (middle and late Devonian, 395–370 m.y.b.p.).

This sequence demonstrates fundamental changes in the characteristics and distribution of continental biocoenoses in spite of some biases induced by the relative paucity of Silurian continental deposits in the areas of intensive investigation (in North America and western Europe). Because of the scarcity of Silurian deposits, the changes between early and late Silurian may be more apparent than real; the "first appearance" of a group in late Silurian or very early Devonian may not preclude an earlier origin, such as the middle or early Silurian. The effects of such potential biases are considered in my interpretation of these phases.

Alluviodeltaic deposits (representing the various aquatic and nonaquatic continental habitats) were particularly widespread from late Silurian through the Devonian in the Laurentian, or "Old Red," continental unit of northwestern Europe, Greenland, and eastern and arctic North America. This obviously has provided the opportunity for a more complete knowledge of continental biocoenoses (as noted above) for this time interval and area. However, discrepancies between the "Old Red" record and that in Australia and in North Africa suggest that the former is not fully representative. These discrepancies are discussed below.

Llandoverian-Wenlockian

Various plant and animal fossils have been ascribed to early and middle Silurian continental ecosystems, though neither age nor habitat have been determined precisely. The oldest traces of likely continental macrophytes appear to be those (1) in alluvial deposits of Virginia (which are probably Llandoverian though they might be as late as Ludlovian; Pratt, Phillips, and Dennison, 1978), (2) in marine deposits of similar or greater antiquity from Maine (Schopf et al., 1966), and (3) in the alluvial Acacus Formation of Libya (which may be late Llandoverian though it could be Wenlockian or even as late as Gedinnian, per Massa, 1980, and Douglas and Lejal-Nicol, 1981). In addition, remains of macrophytes and of possible continental macrozoans occur in Scottish rocks that might be as old as Llandoverian (Lamont, 1948) but are more likely of Wenlockian or even Ludlovian age (Westoll, 1950; Denison, 1956); they apparently represent deposition in transitional marine-to-freshwater habitats (Denison, 1956; Waterston, 1979).

The plant materials include macrophytic algae, probably chlorophytes, from Scotland (Lang, 1937; Niklas, 1976b, 1980), nematophytes from Virginia and Scotland (Pratt, Phillips, and Dennison, 1978; Lang, 1937), and tracheophytes from Libya (Boureau, Lejal-Nicol, and Massa, 1978) and, possibly, from Maine (Schopf et al., 1966). The chlorophytes are almost certainly aquatic, probably freshwater, and possibly brackish-water but interpretation of the nematophytes is somewhat more problematic. Although Lang argues for a fully terrestrial habit, the evidence does not require such a conclusion (Edwards, 1980). The occurrence of the nematophytes in the rocks requires some to have been nonmarine (though not necessarily non-aquatic), but it does not exclude the possibility that some were brackish-water or even marine plants (Smith, 1979). Their morphology (Lang, 1937; Pratt, Phillips, and Dennison, 1978) and their geobiochemistry (Niklas, 1976a; Niklas and Pratt, 1980) imply adaptation to subaerial conditions but possibly as emergent hydrophytes and/or as littoral and riparian plants (Gray and Boucot, 1977, 1978). The argument for extensive occupation of terrestrial habitats is further weakened by lack of attachment to any sort of basal absorptive organs and by the absence of scleritized tissues necessary to support an erect habit.

The presumed macrophytes from Maine consist of small, simple, erect axes and occur in strata that otherwise bear near-shore assemblages of marine fossils (Schopf et al., 1966). Although Strother and Lenk (1983) argue that they represent worm burrows, they possess a coalified outer layer suggesting thick-walled cells, and their chemical composition resembles that of some late Silurian and early Devonian tracheophytes (Niklas, 1980). The form of the axes resembles that of early tracheophytes, so they might be regarded as representing "prototracheophytes" (Edwards, Bassett, and Rogerson, 1979; Raven, 1977) though lack of preserved microstructure prevents a test of this suggestion. Their habitat was most likely littoral marine though neither sublittoral nor supralittoral interpretations can be excluded.

The plant fossils from Libya clearly represent tracheophytes, though small and relatively simple ones. They are clearly adapted for terrestrial as well as semiterrestrial habits, but their geologic age is in considerable doubt, as noted above. They occur in otherwise unfossiliferous continental deposits that overlie Middle Llandoverian marine deposits and underlie Siegenian marine units; they might be the lateral time equivalents of Late Llandoverian and Wenlockian marine deposits present in a separate basin to the north. The plants consist, however, of genera characteristic of Siegenian and post-Siegenian strata in Europe and North America, although forms of similar evolutionary grade have been assigned a Ludlovian date in Australia (Douglas and Lejal-Nicol, 1981). In terms of my analysis of ecosystem development, the most conservative viewpoint would seem to accept the presence of a few small, primitive tracheophytes in early Silurian continental biocoenoses.

In addition to plants, the mid-Silurian continental rocks of Scotland have yielded what is probably a brackish-water fauna with an admixture of possible freshwater and terrestrial elements (Denison, 1956; Waterston, 1979). The assemblages include ostracods, eurypterids, limulids, scorpions, myriapods, and fish in addition to lingulid brachiopods. The ostracods represent genera that appear elsewhere in transitional marine-nonmarine situations; the limits on their distribution are uncertain but likely extend to brackish-water habitats (Hoskins, 1961). Some of the eurypterids may have been amphibious (for example, *Drepanopterus*, per Størmer, 1976, and Rolfe, 1980, though Watenston, 1979, suggests they were predominantly aquatic), and several of the genera represent the "brackish phase" eurypterids of Kjellesvig-Waering (1961). The scorpions show no trace of book lungs and may have been gill-bearing (Laurie, 1899); like other known pre-Carboniferous scorpions they were probably aquatic or semiaquatic (Størmer, 1976). The myriapods are conventionally considered to be terrestrial, though Størmer (1976) suggests that an early Devonian one from Germany might have been amphibious. The fish consist entirely of primitive, jawless types — agnathans, including anaspids, thelodonts, and osteostracians. In the late Silurian these groups typically appear in brackish-water assemblages, although some occurrences may represent freshwater habitats or at least include individuals transported from such situations (Denison, 1956).

The evidence from early and mid-Silurian sedimentary rocks thus demonstrates the presence and some of the general features of continental ecosystems. Macrophytes were probably present as producers in both aquatic and terrestrial ecosystems and probably included forms with rhizome-rhizoid systems for water and nutrient collection. At the very least, the presence of macrophytes would have tended to stabilize the amount of living biomass and of detritus available to animals and decomposers, as in modern ecosystems (Cummins, 1975). They would have increased primary production by drawing on nutrients and water from the substrate, as well as by utilizing the greater intensity of light available to emergent hydrophytes and subaerial plants. To the extent that they utilized terrestrial habitats, they would have supplied allochthonous detritus to aquatic habitats and increased the rate of nutrient release through accelerated weathering. Rhizome mats associated with littoral, riparian, and terrestrial macrophytes could have damped episodic erosion and deposition to some extent and might have reduced variations in runoff and throughflow.

These deductions are consistent with changes observed in the consumer components of continental ecosystems. Brackish-water assemblages are far more common in the early and middle Silurian than in the Ordovician and include a greater abundance and diversity of animals, among them meiodetritivores (ostracods and, possibly, myriapods), meiopredators (scorpions), and macrodetritivores (limulids and some variety of agnathan fish). In addition, the eurypterid invasion of brackish water added macropredators (though some eurypterids were detritivores, per Waterston, 1979, 316–17). Three trophic levels and a major decomposer-detritivore loop are clearly distinguishable; the scorpions, which are large enough to have fed on other (unfossilizable) meiopredators, may represent the fourth level, as may some eurypterids. Many of the latter, however, were probably largely dependent on macrodetritivores and were thus effectively of the third, rather than the fourth, trophic level. Parallel though less extensive changes had occurred in freshwater ecosystems if, as Denison (1956) suggests, some of the agnathan fish actually lived in freshwater habitats. In addition, some of the myriapods and scorpions may also represent freshwater ecosystems — the former along with some fish filling the second trophic level (as detritivores) and the latter the third level (as predators on the meiobiota). Terrestrial biocoenoses, though very poorly known from lower Silurian fossil assemblages, probably included some small vascular plants (tracheophytes) as well as various microphytes. Some (or all) of the millipedes represent the second trophic level and, if some of the scorpions were amphibious, they would have operated at the third level as meiopredators. The absence or rarity of small arthropods in early freshwater and terrestrial assemblages has little positive significance since the probabilities of their fossilization and discovery are diminishingly small. Only three significant occurrences have been reported from the Devonian under much more favorable circumstances for discovery. Algal crusts could have supported some abundance and diversity of such forms and their occurrence in two early Devonian assemblages (see below) suggests their presence and differentiation by late Silurian if not considerably earlier (Rolfe, 1980).

On the other hand, any increases in productivity and reductions in stress and uncertainty in continental ecosystems could not have been very great. Carbonaceous accumulations (coaly lenses and carbonaceous shales) remained very rare in continental sediments until the late Devonian. The continued relative dominance of braided-stream deposits into Devonian time (Cotter, 1978) speaks for persistence of flashy stream discharge, for abrupt, erratic erosion and deposition, and thus for general instability in terrestrial, freshwater, and even brackish-water habitats. The paucity of continental fossil assemblages also points toward low productivity (if not high stress and uncertainty as well).

Ludlovian-Pridolian

The best-known late Silurian continental assemblages occur in the Welsh borderland of the British Isles and are supplemented by occurrences in Scotland, Norway, Spitsbergen, and eastern North America. The Libyan localities discussed above and those in Australia which yield the "Baragwanathia flora" may also date to the late Silurian (Garrett, 1979; Boucot and Gray, 1982). Although dominated by deposits representing marine to brackish-water transitional habitats, the known assemblages do include some upper-estuarine and freshwater situations. Unfortunately, the latter are relatively late (Pridolian), so evolutionary sequences cannot be detailed and the Ludlovian-Pridolian interval must be treated as a whole.

Although interpretation of the producer components is confused by the disputed dating of the early fossil plants from Libya and Australia, it is accepted that tracheophytes appeared at least as early as Ludlovian, as attested by bundles of tracheids and by small tracheophyte-like axes from the British Isles and eastern North America (Edwards and Davies, 1976; Edwards, Bassett, and Rogerson, 1979). These plants were all quite small with axial diameters of about 3 mm, had a simple morphology with leafless, dichotomous branches (Chaloner and Sheerin, 1979), and are assigned to the rhyniophytes. Their basal portions are unknown, but rhizomes and rhizoids appear on similar axes from Gedinnian deposits and thus are presumed to have been present in late Silurian forms (Edwards, 1980). The Libyan and Australian occurrences demonstrate the existence of other tracheophytes, specifically the trimerophytes and the lycopsids. The former are distinguished by multiple, unequally branching, leafless axes. The lycopsids are relatively complex forms marked by elaboration of branching and by development of vascularized leaves arising from the surface of the branches. These features would have increased the effective area for photosynthesis and simultaneously required increased nutrient and water uptake from the soil. Although all these fossils derive from near-shore marine and adjacent continental margin deposits, they probably reflect the composition of continental ecosystems as a whole since they provide a sufficient source for the limited variety of trilete spores dispersed through these same deposits; there is no evidence of "exotic" spores transported in from different types of upland plants (Chaloner, 1972; K. C. Allen, 1981).

Nematophytes and algae (see preceding section) occur in considerable numbers in many of the late Silurian continental assemblages, along with remains of early tracheophytes. Lang (1937) interpreted these assemblages as terrestrial but, since they represent plant fragments transported to their burial sites, they may be an admixture of aquatic and nonaquatic species derived from freshwater or even brackish habitats as well as terrestrial (Edwards, 1980). The first fossil charophytes, a group whose modern representatives are all submerged, freshwater macrophytes, also appear in these deposits (Croft, 1952).

Brackish-water fossil assemblages include the same major animal groups known from the middle Silurian (see discussion of mid-Silurian inliers of Scotland above) plus some significant additions. Holdovers include lingulid brachiopods, ostracods, eurypterids, limulids, and possibly scorpions among the arthropods, and anaspids, thelodonts, and osteostracians among the agnathan (jawless) fishes (Denison, 1956, 372–74; Allen and Tarlo, 1963; Kjellesvig-Waering, 1961). In addition, some bivalves and snails occur in what seem to have been brackish-water situations (Allen and Tarlo, 1963), and heterostracian agnathans apparently began to invade brackish (and freshwater) habitats by Pridolian time (Denison, 1956, 419–20; Allen and Tarlo, 1963). Finally, and probably most significant from both ecologic and evolutionary viewpoints, primitive jawed fish (the acanthodians) make their first appearance in brackish assemblages at least by Pridolian time (Allen and Tarlo, 1963).

By late Silurian, freshwater fossil assemblages are somewhat more easily distinguished from brackish-water ones. Indeed, Allen and Tarlo (1963) recognize several distinct assemblages in the lagoon-estuary-river-lake habitat spectrum of the Old Red Sandstone in the Welsh borderland. In spite of this increased differentiation, most of the major groups are the same as those in brackish-water assemblages. These probably include some ostracods, eurypterids, and limulids as well as scorpions (see Allen and Tarlo, 1963, and Denison, 1956, 372–74, *contra* Kjellesvig-Waering, 1961) and may also include some myriapods (Størmer, 1976). The osteostracian and anaspid agnathans also continue in freshwater biocoenoses from mid-Silurian time, albeit somewhat more diverse and more widely distributed than in late Devonian deposits. Newcomers include heterostracian agnathans (previously predominantly or entirely marine) and primitive jawed fish, the acanthodians. In addition, freshwater biocoenoses very possibly contained a variety of small arthropods that have not been observed so far (except for ostracods) but do appear, very rarely, in early Devonian assemblages.

Fully terrestrial faunas are very poorly known, though a few of the fossils preserved in aquatic assemblages were probably of terrestrial or semiterrestrial organisms. These consist of arthropods (first known from mid-Silurian occurrences), some fully terrestrial myriapods, and amphibious scorpions, eurypterids, and limulids. In addition, terrestrial biocoenoses probably included a meiofauna of small arthropods and various "worms" inhabiting the soil, algal crusts, and any litter accumulations generated by the now developing terrestrial macrophyte communities.

Overall, the most significant transformations in taxonomic composition between mid- and late Silurian continental ecosystems are (1) the expansion (or first appearance) of tracheophytes, (2) a modest diversification of brackish and freshwater fish, and (3) the appearance of large predators (jawed fish and possibly eurypterids) in freshwater habitats. The direct contribution of tracheophytes to primary production was probably limited by their small size and by the lack of well-differentiated foliage and true root systems. Further, they were probably quite limited in geographic and habitat distribution, as indicated by their rarity as fossils and by restriction of fossil occurrence to lower-alluviodeltaic deposits. In addition, within-habitat diversity was quite low (Edwards, 1980; Niklas, Tiffney, and Knoll, 1980). To the extent that the tracheophytes and, possibly, the nematophytes utilized terrestrial sites, they could have contributed to nutrient release in weathering, to retention of water in soils (Edwards, 1980, 75–76), to reduction of erosion, and to the supply of organic detritus for adjacent aquatic habitats. These groups plus the charophytes must also have been the major producers in aquatic habitats. By cycling mineralizing nutrients from the substrata, they may have wrought a modest increase in microphyte productivity as well. In all, primary production in continental ecosystems was almost certainly higher in late Silurian than in early Silurian.

The increase in abundance of animal fossils suggests an increase in secondary production, and the increase in variety of consumers demonstrates increased trophic diversity within brackish and probably freshwater ecosystems. The apparent increase in within-habitat diversities involved an increase in the number of distinct feeding types ("guilds"), as well as in the number of species within such guilds. Although the anaspid fish continued primarily as feeders on the nektonic meiofauna (Denison, 1956, 422–23, and 1961), with the appearance of cephalaspids and ateleaspids the osteostracians showed increased specialization for bottom-living, mud-grubbing habits (Westoll, 1979; Denison, 1956, 422). An increase in the variety of limulids and eurypterids also added to the diversity of large detritivores. The appearance of heterostracians and acanthodians in continental biocoenoses increased the diversity of forms feeding on the nektonic meiofauna (Denison, 1956, 419–20, 425–26, and 1961; Halstead, 1973). In addition, some of the acanthodians may have functioned as macropredators (Denison, 1956, 425, and 1979); these, together with some predatory eurypterids, may represent further differentiation of the fourth trophic level, though clearly this had not reached the level it was to attain by the end of the early Devonian.

The record of terrestrial ecosystems, so far as it goes, suggests that a rather sparse population of tracheophytes and some nematophytes occupied riparian and littoral sites and may have persisted through the dry seasons on the sites of ephemeral flood-basin ponds. Such marginally terrestrial ecosystems probably included some myriapods as detritivores and some of the amphibious scorpions and eurypterids as predatory foragers from adjacent aquatic habitats. Collembolids, mites, and mitelike forms occur in slightly younger assemblages and probably functioned as meiofaunal detritivores, herbivores, and predators; their absence from the Ludlovian-Pridolian is very likely an accident of sampling because such fossils are typically very rare even in post-Devonian deposits.

In summary, the fossil record shows clearly that brackish and freshwater ecosystems were well developed by the late Silurian. Although they may not have been much different from mid-Silurian ones, they are quite certainly different from those of the middle and late Ordovician. Brackish-water ecosystems apparently had relatively dense and diverse populations, including large detritivores and herbivores (agnathans and limulids) at the second and third trophic level and probably some fourth-level predators (acanthodians and eurypterids). Freshwater ecosystems, though less well represented, show similar patterns. Macrophytes had begun their deployment in terrestrial ecosystems, presumably with some effect on the micro- and meiofauna, but these forms are so inadequately represented by fossils that detailed inferences are impossible. However, these terrestrial macrophytes probably contributed to changes in aquatic ecosystems, through increases in nutrient release and in supply of organic detritus; they may also have reduced physical disturbance and instability in both aquatic and nonaquatic habitats by their effect on runoff, water storage, and erosion.

Gedinnian-Emsian

Marked changes occur in early Devonian continental assemblages, particularly those from freshwater and terrestrial habitats. Although some of this transformation may reflect more complete sampling, much of it represents real evolutionary innovation, particularly among tracheophytes and fish. For example, trilete spores are likely to be widely dispersed into marine as well as continental deposits and thus be least affected by sampling bias. They show a progressive increase in morphologic complexity and double in generic diversity from Pridolian to Gedinnian, double again in the Siegenian, and still again in the Emsian (Chaloner, 1972).

Late Silurian coastal lowland plant associations continued into the early Devonian but with some increases in morphological complexity, diversity, and size (Chaloner and Sheerin, 1979; Niklas, Tiffney, and Knoll, 1980; Knoll et al., 1984). In addition, lowland sediments yield some spores that cannot be attributed to the associated plant megafossils, thus implying transport from upland sites (K. C. Allen, 1981) and the appearance of an "upland" tracheophyte flora.

Radical changes also appear in the faunal record with the first appearance of a considerable variety of small arthropods (representing both nonaquatic and aquatic biocoenoses) and with the addition of a large number of new kinds of jawed fishes to the brackish and freshwater assemblages that continued from the late Silurian. As noted above, many (or all) of these small arthropods may have been present in middle Silurian (or even pre-Silurian) continental biocoenoses, though they have not yet been discovered as fossils. The timing of their first appearance may therefore have little ecologic or evolutionary significance. On the other hand, the appearance of the new groups of jawed fish must demonstrate a major change in aquatic ecosystems, for fossils of such fish would have almost certainly been found in late Silurian deposits if they had been present in ecologically significant numbers.

The characteristic Silurian brackish-water assemblages (of lingulids, ostracods, eurypterids, limulids, scorpions, anaspids, osteostracians, acanthodians) are modified by the occurrence of three major new taxa of jawed fish, the arthrodires, the crossopterygians, and the dipnoans, and by the further diversification of the jawless heterostracians (Størmer, 1976). The arthrodires and crossoptarygians represent predators that presumably fed on small fish and large invertebrates (discussed below). Early dipnoans (lungfish) also appear in some transitional marine-brackish situations, but not in fresh water, probably as predators on worms and arthropods (Denison, 1956, 429–30).

Freshwater assemblages of early Devonian age include a considerable variety of small crustaceans in addition to ostracods, fish, and (possibly) limulids. The crustacean fauna is dominated by brachiopods, including clam shrimps (Conchostraca) and fairy shrimps (Anostraca), as well as two orders, Lipostraca and Acercostraca, known only as fossils (Tasch, 1959, 140–41, 151–53, 159, 183–85). Among the jawless fish, the osteostracians (cephalaspids, ateleaspids, and two new groups, the kieraspids and galeaspids) continued in their benthic, mud-grubbing habitus; the freshwater heterostracians increased in abundance and diversity (for example, Halstead, 1973, 320–24), with new specializations for different feeding sites and different kinds of food items (Denison, 1956, 418–20; Halstead, 1973). Three orders of jawed fish representing at least two distinct classes — the acanthodians, the arthrodires, and the crossopterygians — are known from freshwater assemblages. The acanthodians are more diverse and abundant in early Devonian than in Silurian assemblages (increasing from one to five families) and, although primarily predatory on the small animals of the meiofauna, must have consumed some relatively large invertebrates and fish (Allen and Tarlo, 1963; Denison, 1979). The arthrodires make their first appearance in freshwater assemblages in the Gedinnian and invade brackish ones only in the Siegenian. The earliest species were probably limited to relatively small prey, such as crustaceans and fingerling fish, but later ones, at least as adults, fed on rather large animals (Denison, 1979). The crossopterygians, represented by only a few genera, also probably fed primarily on other fish (Denison, 1956, 428–30).

Early Devonian terrestrial faunas include myriapods (some possibly amphibious in habit; Størmer, 1976), collembolids, mitelike trigonotarbids, true mites (acarids), and spiders (Størmer, 1970, 1976; Scourfield, 1940; and summaries in Kevan, Chaloner, and Savile, 1975; and Rolfe, 1980). Generally these are types of animals that now inhabit soil and plant litter, some of them consuming algae, fungi, and bacteria, and others nematodes and other small arthropods (Rolfe, 1980). Though Kevan, Chaloner, and Savile (1975) suggest that some or many of these Devonian organisms fed on plant sap and spores, Rolfe (1980) questions their conclusion. In addition, some limulids, eurypterids, and scorpions may have foraged in terrestrial habitats (Størmer, 1976).

The early Devonian deposits of southern Britain have provided the most detailed information on specific continental habitats in the range from "proximal" (piedmont) and medial alluvial facies to the distal alluvial (lower delta plain) and coastal ones (J. R. L. Allen, 1979). The upland border or proximal facies consist primarily of playa, mudflow, and low-sinuosity channel deposits representing flashly hydrologic regimes; since they yield no plant fossils and only a few animal burrows, it appears that most aquatic and riparian macrophytes (and their accompanying consumers) were not yet able to invade such low-resource/ high-stress habitats (Edwards, 1980). The medial alluvial facies also derive from low-sinuosity streams but seem to represent more stable habitats. In addition to drifted plant fragments they include dense, monospecific plant accumulations that suggest local stands of these plants on stream banks, upper portions of bars, and/or backwater swales (Edwards, 1980). Animal fossils include some fish remains, which are generally disarticulated and water-sorted, and an abundance and variety of trace fossils. No arthropods are reported, but the depositional situation was a poor one for preservation of small and/or delicate skeletons. The distal alluvial facies represents deposition by sinuous streams. Channel and channel-margin deposits yield drifted plant remains and many fish, including some pockets of articulated individuals associated with abundant plants in what may be swale deposits. In contrast, the overbank mudstones (nominally flood-basin swamp and pond habitats) yield only trace fossils as the sole remnants of an autochthonous biota and scattered, drifted plant remains.

The transformations in the composition of continental biocoenoses and in the characteristics of continental ecosystems in the early Devonian are parallel to, but much more extensive than, those noted for the late Silurian. The most significant changes in composition (so far as ecosystem development is concerned) include (1) increase in abundance, diversity, and morphological complexity of semiaquatic and terrestrial plants, primarily tracheophytes; (2) increase in variety and abundance of aquatic and terrestrial meiofauna, primarily arthropods; and (3) increase in abundance and variety of aquatic macrofauna, primarily heterostracian and gnathostome fishes. These presumably reflect increases in primary production, reductions in disturbance and instability, and alterations in trophic structure and dynamics.

The changes in the continental floras were almost certainly basic to those in consumer populations and to the major alterations in the ecosystems. The increased abundance and wider occurrence of macrophytes clearly demonstrate that primary production was greater in the early Devonian than in the late Silurian, although primarily limited to riparian and lake-margin situations in alluviodeltaic lowlands. The rhizome system of early tracheophytes (particularly if associated with mycorrhizae and mycotrophism, as suggested by Pirozynski and Mallock, 1975, and as implied by some fossil material from the Rhynie Chert of Scotland) and the chemical environment created by decomposition of plant litter would have increased release of nutrients from the substrate. This in turn would increase the potential concentration of nutrients in the surface water and in the associated aquatic and terrestrial biomass. These changes, together with the recycling of buried nutrients by rooted hydrophytes, would also have increased the potential nutrient supply for aquatic microphytes and hence their productivity. In addition, the extensive development of prostrate rhizomes with rhizoids must have stabilized terrestrial soils and aquatic sediments against rapid erosion (Edwards, 1980) and damped variation in soil water, surface runoff, and stream flow, at least in relatively well vegetated lowland areas. Such vegetational cover (and the associated plant litter) would also have provided some protection against water loss and temperature variations for small organisms as well as some stability in food supply. On the other hand, the character of the earliest Devonian tracheophytes — for example, their small size and the lack of leaves and true roots in many groups — suggests that primary productivity was still relatively low and moderation of physical disturbance and uncertainty was rather limited. These latter conclusions accord with the apparent limitation of tracheophytes to medial and distal alluvial facies and, probably, to riparian and channel swale situations.

Consumer populations in freshwater biocoenoses changed markedly, whereas similar changes in brackish-water and terrestrial consumers (and ecosystems) appear less ecologically significant. In freshwater ecosystems, the expansion of invertebrate consumers (at second and third trophic levels) is reflected not only in occasional body fossils, but more clearly in the abundant and varied trace fossils, even in overbank pond habitats. Fourth-level macropredators — such as acanthodians, arthrodires, and crossopterygians — were rare or nonexistent in earlier freshwater ecosystems but are relatively abundant and diverse in Devonian ones. Diversification within habitats at the second and third levels (heterostracians and some acanthodians and arthrodires) must also indicate significant changes in trophic structure and/or habitat characteristics. This general pattern is further confirmed by the appearance of a variety of small arthropods as primary consumers (though the total absence of comparable forms from earlier assemblages might be ascribed more to inadequate sampling than biologic reality). The increase in fossil abundances further suggests a significant increase in secondary production.

In constrast, the consumers in terrestrial ecosystems apparently consisted largely or entirely of small animals operating on the second trophic level (with a preponderance of detritivores over herbivores), with a modest variety of small predators on the third trophic level. Any comparison with late Silurian terrestrial consumers is dubious, however, since the absence of a meiofauna from that interval may be a function of limited and biased sampling. Although one might expect that some changes occurred in consumers consequent on expansion of terrestrial macrophyte populations, the characteristics of these early Devonian fossil representatives suggest their continued limitation by low or episodic primary production and by intense physical disturbance.

Brackish-water ecosystems, in spite of greater diversity at the third and fourth trophic levels and some large changes in taxonomic composition, show only rather minor changes in basic characteristics, for example, in trophic structure. Thus it appears that the diversification of brackish-water ecosystems was largely accomplished by the end of the Silurian — in contrast to that of the freshwater ones, in which diversification continued through the Devonian.

Eifelian-Famennian

The tracheophyte "green revolution" progressed through the middle and late Devonian with the development of rooted plants and the appearance of shrubs and trees in terrestrial habitats, and with the further enrichment of freshwater ecosystems. Known faunal changes were concentrated largely in brackish-water and freshwater fish; terrestrial faunas, so far as they are known, show relatively little modification in composition — late Devonian and early Carboniferous amphibians appear more closely tied to aquatic ecosystems than to terrestrial ones (Olson, 1971, 631, 634–36).

Among the tracheophytes, large, pinnate leaves appear in the Eifelian with the evolution of progymnosperms and pteropsids. Some representatives of these groups as well as of the lycopsids reached tree size and had well-developed root systems and foliage crowns (Chaloner and Sheerin, 1979). Both progymnosperms and lycopsids developed heterospory, with a very much enlarged megaspore providing a food reserve for the gametophyte and embryonic sporophyte — a feature that would be desirable where shade from a plant canopy limited seedling survival and growth (Chaloner and Sheerin, 1979). Development of foliage and increase in size required (or depended on) transformations in structure of the tracheids, reorganization of the xylem, and alteration in growth pattern (Banks, 1970, 97–90; Chaloner and Sheerin, 1979). Smaller plants persisted among the lycopsids and evolved in the pteropsids, though some primitive groups of small plants (for example, rhyniophytes) diminished in importance after the Eifelian (Chaloner and Sheerin, 1979). As a result, spatial stratification appeared in terrestrial communities (Niklas, Tiffney, and Knoll, 1980; Tiffney, 1981; Edwards, 1980; Chaloner and Sheerin, 1979), with possible implications for the emergence of winged insects in the Carboniferous.

In brackish and freshwater biocoenoses, the vertebrates underwent considerable change. Agnathans, both osteostracians and heterostracians, diminish progressively through the later Devonian (Westoll, 1979) with only a few persisting until the Frasnian. Some of the benthic, detritus-feeding niches were filled by the antiarchs, which derived from an arthrodire stock in Siegenian and are the commonest fish fossils in most middle and late Devonian freshwater deposits. Arthrodires continued as medium-size predators; acanthodians maintained a similar role. The osteichthians underwent the most marked changes — the appearance of the first ray-fins (actinopterygians), the invasion of fresh waters by lungfish (dipnoans), and a radiation of the crossopterygians (Westoll, 1979). The early actinopterygians were small- to medium-sized fish and were probably primarily predators on small nektonic and benthic animals, apparently filling heterostracian-like roles in part. The lungfish seem to have been dominantly selective bottom feeders, fitted to prey on tough-shelled crustaceans and on annelids (Denison, 1956, 429–30). The crossopterygians were medium- to large-sized nektonic predators that as adults must have fed on other fish and large invertebrates. In addition, some or all of the early amphibians (known from two Frasnian trackways and a few Famennian skeletons) probably fed primarily or entirely in aquatic habitats on similar types of prey (see discussion below).

Mid- and late Devonian freshwater and terrestrial arthropods are less well known than early Devonian ones — though, obviously, groups with both early Devonian and post-Devonian occurrences must have been present: for example, the fairy and clam shrimps among the crustaceans; the scorpions, acarids, trigonotarbids, and spiders among the archnids; the myriapods; and the collembolids. Kevan, Chalone, and Savile (1975) suggest that many of the modifications in structure and size in mid- and late Devonian plants represent adaptive responses to attack by an increasing number of herbivorous arachnids and hexapods. On the other hand, eurypterids seem to have declined in significance after the early Devonian; for example, twelve genera are reported from late Silurian and fifteen from early Devonian but only nine from middle and eight from late Devonian (Størmer, 1955).

Whether any of the early amphibians foraged in terrestrial ecosystems is uncertain; they may have been primarily transients on their way from one pond to another. Certainly the skeletons known from the very late Devonian, with their large size and fishlike teeth, jaws, and tail, suggest animals that, at least in their adult stage, fed primarily or entirely on fish and large aquatic invertebrates and traveled over land primarily to feed in scattered freshwater habitats (Olson, 1971, 635–36). On the other hand, juvenils of these species might have foraged for small terrestrial as well as aquatic invertebrates, and some species with small, arthropod-feeding adults may well have been present in riparian sites.

These changes in freshwater and terrestrial biocoenoses imply significant transformations in ecosystem structure and dynamics. In particular, the appearance of tree-shrub communities (open forest?), at least in well-watered coastal lowlands, implies an enlarged food supply for terrestrial herbivores and an increased export of organic detritus as well as dissolved nutrients to aquatic ecosystems. In addition, their presence would have further moderated physical disturbance and instability in aquatic as well as terrestrial habitats, although the total effect may have still been relatively small because of the limited geographic extent of such forests. Finally, to the extent that tracheophytes, particularly trees, spread into the continental interiors, the increased return of moisture to the atmosphere through transpiration and the reduction in terrestrial albedo in the tropics may have broadened the extent of tropic, wet climates and diminished that of subtropical dry climates (see discussion by Charney, Stone, and Quirk, 1975).

The transformations in freshwater ecosystems, presumably induced by their coupling with terrestrial systems, are striking. They include not only continuation of earlier trends in trophic differentiation and specialization but also the appearance of new trophic tactics, that is, foraging among scattered, isolated aquatic habitats by amphibious vertebrates. At the second and third trophic levels the agnathans were replaced (or displaced) by antiarchs, arthrodires, and actinopterygians, but the available evidence is not adequate to demonstrate any other changes at this level — for example, changes in productivity or in number, type, or breadth of niches. However, the radiation of crossopterygians suggests significant changes at the third and fourth levels. This may have involved one or more of the following: (1) increased supplies of previously rare food items, (2) utilization of previously inhospitable habitats, and (3) splitting and narrowing of niches. If, as suggested above, the early amphibians fed primarily by foraging among small, more or less isolated aquatic ecosystems, they would effectively have added another trophic level (the fourth) to many of those systems as well as competing with crossopterygians for niches in other aquatic habitats.

The effects of eutrophication also appear in the assemblages representing large lakes. For example, Donovan (1980) ascribes the abundant and diverse fish faunas of the middle Devonian of Caithness in Scotland to a deep, eutrophic tropical lake supporting three or four link food chains based on primary production by pelagic microorganisms. The absence or at least rarity of such ecosystems before the middle Devonian may be attributed to a low input of detritus and dissolved nutrients prior to development of an extensive cover of land tracheophytes, together with their bacterial and fungal consorts.

Changes in terrestrial ecosystems are obscured by the rarity of terrestrial arthropods in middle and late Devonian fossil assemblages and by the very limited evidence for amphibian evolution and ecology. As already noted, Kevan, Chaloner, and Savile (1975) interpret some features of the plants as indicative of increased consumption by arthropods, and thus of the presence of such forms in the biocoenoses if not in the fossil record. In particular, they suggest that the diversification of the hexapods and the initial stages in evolution of winged insects were coupled with changes in the flora. (Recent discoveries of arthropods in the late Devonian of New York seem to support some of these suppositions; Shear et al., 1984). As suggested above, some of the early amphibians may have utilized terrestrial arthropods as a major food source at the third and fourth trophic levels. The fossil record gives no positive evidence for this inference, however, and in any case the extreme rarity of tetrapods in late Devonian assemblages is presumptive evidence against a major role for macroconsumers (at the fourth trophic level) in terrestrial ecosystems.

Overall, late Devonian continental ecosystems were characterized by further differentiation and expansion of consumers at the third and fourth trophic levels, although this is better documented for freshwater than for brackish or terrestrial habitats. This change was associated with a very marked diversification of terrestrial tracheophytes, along with an increase in their abundance and an expansion in their habitat range. These transformations presumably increased primary production in terrestrial habitats and the supply of dissolved nutrients and organic detritus to aquatic ones, but the rarity of large accumulations of plant debris (preserved as coals) demonstrates that productivity had yet to reach the level attained in the Carboniferous and later. Changes in secondary production are more difficult to demonstrate, but in aquatic assemblages the increased abundance and diversity of animals at the top trophic level argues for higher production at intermediate levels. This conclusion presumably is supported by concentration in aquatic habitats of increased plant detritus from terrestrial habitats. Conversely, the apparent absence, or near absence, of macropredators from terrestrial ecosystems until the mid-Carboniferous points toward low secondary production or a temporal lag in evolution of terrestrial consumers.

Patterns in Development

Directions of Change

The geologic record demonstrates an increase in the number and variety of fossils and fossil assemblages representing continental ecosystems from the Ordovician through the Devonian; it also demonstrates changes in associated sedimentary rocks that reveal biological effects on weathering, erosion, and deposition. Analysis suggests that these changes involved large-scale transformations in (1) trophic structure and dynamics, (2) habitat utilization, and (3) ecological strategies of brackish, freshwater, and terrestrial ecosystems. These inferences are documented primarily by macrofloral and macrofaunal fossils but are also consistent with the limited number of meiofaunal samples and with changes in depositional style related to abundance and distribution of plants. In addition, they are compatible with deductions about early continental habitats drawn from the absence or extreme rarity of fossils.

At their first appearance, assemblages in all three types of continental habitat are very rare, consist of relatively few fossils, include few if any forms that might have fed at the fourth trophic level, and show little variety even at the third level. Deposit/detritus feeders (at the second and third trophic levels) predominate although they display little diversity. In addition, the sediments show little evidence of biologic activity — for example, the accumulation of reduced carbon, changes in the intensity and mode of chemical weathering, changes in bioturbation or in the patterns of alluvial deposition. Overall, trophic structure, at least as represented by macrofossils, was relatively simple; there was (1) little differentiation between second, third, and fourth levels, (2) little diversification and specialization within levels, and (3) a dominance of detritus as a food source.

Brackish-water assemblages display these "primitive' characteristics at their first appearances in the Ordovician but undergo progressive changes in the Silurian and Devonian; such assemblages are rare through the middle Silurian but are common thereafter. Although evidence for early and middle Silurian biocoenoses is scanty, the fourth trophic level was clearly differentiated by this time, and there is some suggestion of diversification at levels two and three. However, deposit feeders remained the dominant trophic type, although some meio- and macropredators were present. Trophic diversification was continued in late Silurian and early Devonian ecosystems with an increase in the importance of predators relative to deposit feeders and with specialization for different kinds of prey and for different feeding sites at each trophic level.

Freshwater ecosystems displayed a similar pattern of development, although lagging behind the brackish-water ones. The earliest assemblages (early and middle Silurian) are rare and represent relatively simple trophic structures. Occurrences in the late Silurian are more common and more fossiliferous, but show that trophic structure was apparently similar to that of mid-Silurian: (1) little diversity or specialization at the second and third trophic levels, (2) little or no differentiation at the fourth level, and (3) dominance of deposit feeders. By the end of the early Devonian, however, the situation had changed: the consumers on the second and third trophic levels had diversified and specialized further by food type and feeding site, and the fourth level was represented by several types of fish and, possibly, by macropredatory arthropods. Diversification and specialization continued into the middle and late Devonian, culminating with the appearance of large macropredators that foraged among separate aquatic habitats as well as within them. In this event, the trophic structure (if not trophic diversity) approximated that present in Carboniferous and younger freshwater ecosystems.

Development of terrestrial ecosystems followed a step or two behind the aquatic. Early and middle Devonian assemblages were probably dominated by small detritus feeders, although some meiopredators (effectively third level) were present. Sampling of those components is so spotty, however, that generalizations about diversification and specialization are impossible. The appearance of the first tetrapods in late Devonian time potentially added a fourth trophic level to terrestrial ecosystems, but the extent of their participation in terrestrial, as opposed to aquatic, food chains is doubtful. Indeed, for terrestrial ecosystems extensive development of the fourth trophic level and diversification and specialization at the second and third is not clearly documented prior to the late Carboniferous.

Primary and secondary production apparently increased in all three habitat regimes in parallel with, or perhaps in advance of, changes in trophic structure. Though the fossil record provides no direct, unambiguous evidence of productivity, inferences from fossil abundance and other biogenic inputs to deposition do provide a semiquantitative measure of change. Where assemblages with similar preservational potential can be compared, relative fossil abundance bears some relation to production. On the basis of such evidence, secondary production increased through the Silurian into the Devonian. In brackish-water ecosystems the change seems most marked from mid-Silurian to early Devonian and may have approached a plateau thereafter. In freshwater systems, abundance rose sharply after the late Silurian/earliest Devonian and continued an upward trend thereafter — perhaps not culminating until the late Carboniferous/early Permian. The increase in macrophyte remains in aquatic assemblages through the Silurian and Devonian probably records an increase both of *in situ* primary production and of import of allochthonous plant detritus; in either case, it marks an increase in energy available for consumers. In terrestrial ecosystems the rapid increase in abundance of terrestrial plant fossils from late Silurian through late Devonian indicates increased primary production. This conclusion is supported by the shift in the dominant mode of alluvial deposition from braided- to sinuous-channel deposits reflecting the influence of the plants on stream discharge and sediment bed and on bank cohesiveness. Increased primary production also implies an increase in secondary production, but fossil evidence for consumer abundance is insufficient to test this inference.

These trends in ecosystem characteristics were apparently associated with major changes in the physical characteristics of continental habitats and in utilization of these habitats. I argued above that pre-Silurian continental habitats

1. were marked by very low availability of resources (nutrients and water),
2. presented very high levels of physical disturbance affecting resource utilization, and
3. were subject to frequent, intense, and rather unpredictable variations in the physical environment.

These constraints on biological activity and organization would have been least significant in near-marine habitats and most severe in terrestrial ones. The inferred increases in trophic complexity and in production during the later Silurian and the Devonian clearly indicate relaxation of some or all of these constraints. The features of Silurian and Devonian tracheophytes demonstrate that some of the change was consequent on new adaptations for acquisition and conservation of scarce resources and for resistance to physical disturbance, but the reduction in physical constraints also involved biogenic modifications of the physical habitats themselves.

For example, in terrestrial habitats the evolution of rhizoid-rhizome and root systems in tracheophytes (and the development of the ectomycorrhizal consortium) must have not only increased nutrients for the individual plants themselves but also augmented and conserved the general stock of dissolved and of organically bound nutrients. Further, the appearance of an herbaceous and later an arborescent plant cover with an associated litter-and-root zone must have reduced water loss, increased humidity near the ground, limited temperature variation, and reduced erosion. In addition to increasing resource availability still further, these modifications reduced desiccation and thermal stress and permitted more effective utilization of soil nutrients by plants and consumption of plant tissues and detritus by animals. Obviously, such environmental amelioration wrought by the appearance of terrestrial plants would have produced a positive feedback; that is, the increase in resources and reduction in disturbance and instability would have facilitated additional plant growth and thus furthered modification of physical circumstances. The overall consequence was a progressive increase in what one might call "ecosystem homeostasis," complementing individual homeostatic capacities.

Parallel changes must also have occurred in aquatic habitats as a consequence of the development of a terrestrial (and riparian) plant cover and the associated litter-root-soil complex. The storage of water in the soils and the high humidity under the plant canopy would have moderated fluctuations in runoff and thus in stream discharge. Reduced erosion of slopes, gullies, and banks (owing to the presence of rhizome-rhizoid and root systems) would have reduced the amount of coarse sediment supplied to streams. The result would have been more rivers with more equitable discharge and more stable channels and bars. These effects would also lead to a stabilization of water level in flood-basin lakes and ponds and to a moderation of fluctuations of turbidity and salinity in brackish estuaries.

These deductions are supported in part by sedimentologic and paleobiologic evidence. As noted above, stream deposition tends to change in character from braided- to sinuous-channel regimes, marking a shift toward less episodic runoff, erosion, and deposition and toward a retention of finer-grained sediment. An increase in the abundance of swamp deposits from the mid-Devonian into the Carboniferous also suggests a change from "flashy" to "prolonged" floods. Further, some of the increase in diversity within assemblages may be due to reduction in disturbance; Grime (1979) suggests that diversity is typically low in habitats subject to frequent, intense disturbance (and/or to low resource availability). The progressive extension of ecosystem distribution during the Devonian into inherently more rigorous (and resource-poor) habitats — for example, those of piedmont alluvial plain

— probably also reflects some reduction in physical stress and disturbance.

Factors in Ecosystem Development

What controlled these patterns of development, namely, the elaborations of trophic structure, the increases in productivity, and the diachrony in phases among habitat types? Moreover, why do complex ecosystems appear later in continental habitats than in marine? Finally, why were so many of the critical changes concentrated in an 80-million-year period (late Ordovician to late Devonian) but still widely dispersed within that interval?

Ecological Constraints

Some of the answers must lie in the relationships of ecosystem structure and dynamics to the general characteristics of continental habitats. Compared with marine habitats, the early continental habitats provided little in the way of readily accessible resources and exposed their occupants to severe physical stress and high spatial and temporal uncertainty. As noted above, resource shortages must have limited primary production and favored resource conservation above expenditures for maintenance, growth, and reproduction. In turn, low primary production would restrict secondary production and favor an emphasis on resource conservation among consumers as well as producers. On the other hand, physical stress and uncertainty would induce low average survivorship and favor (or require) an emphasis on replacement (growth and reproduction); such emphasis runs contrary to an emphasis on conservation. With low resources for production and with high requirements for replacement, only a small number of individuals could maintain themselves; consumer populations were limited to the lower trophic levels (where resources were most abundant) and to the most readily available type of food at each level; consumers would also tend to feed as generalists within and among levels. In addition, unpredictable variations in physical factors would produce marked fluctuations and tend to destablize food chains, particularly long ones where disruption would have been multiplicative (see Pimm and Lawton, 1977). The overall result in ecological time was to limit the number of trophic levels and the number of potential niches at each level. (The emphasis on conservation and/or replacement also had consequences in evolutionary times, as described in the following section.)

Some of the adaptive innovations that appeared in the evolution of continental macrophytes increased their access to resources and reduced the effects of physical stress and instability on resource utilization and on survival. This led to a slow shift in emphasis in adaptation from conservation and replacement to resource acquisition (or to competitive preemption) and to maintenance; this shift led to the appearance of a plant canopy, a thick, widespread litter zone, and an equally extensive development of subterranean rhizomes, rhizoids, roots, and ectomycorrhizae. These features increased "ecosystem homeostasis" through conservation of water and nutrients, through reduction of temperature extremes, and through modification of erosion and deposition. The increase in net primary production allowed an increase in secondary production; cumulative increases in primary and secondary production added to the supply of each kind of potential food item as well as to the total number of kinds of food. The moderation of physical stress and uncertainty reduced requirements for reproduction; it also reduced the fluctuations in population densities and the consequent destabilization of food chains. Overall, the result in ecologic time was an increase in the potential number of trophic levels and of niches at each level. In evolutionary time, these changes favored increased specialization of organisms and niche splitting. This led, in ecologic terms, to increased trophic differentiation, specialization, and diversification.

What of the differences among brackish, freshwater and terrestrial ecosystems in the timing of ecosystem development? The rather moderate levels of physical stress and of uncertainty, and the high influx of nutrients and water from a marine reservoir, account for the precocious emergence of advanced, complex brackish-water ecosystems. Freshwater ecosystems, which were subject to more physical stress and disturbance than brackish ones and which were much more dependent on release of nutrients from terrestrial habitats, were somewhat slower to develop. On the face of it, the belated emergence of the upper trophic levels in terrestrial ecosystems (really not until mid-Carboniferous) could be ascribed to the high intensity of habitat stress and uncertainty, rather than to resource supply, which should be roughly equivalent in freshwater and terrestrial habitats. On the other hand, a gross increase in biomass of terrestrial vascular plants does not insure an increase in assimilation by terrestrial consumers; much of this biomass (and much of net primary production) must have consisted of tissues of low nutritive value (high fiber/low protein), compared with the decomposing detritus and the primary production available to aquatic consumers. Thus, the evolution of terrestrial herbivores might have been hindered and delayed by these and other unfavorable characteristics of vascular plants as food sources. Therefore the middle and late Devonian increases in terrestrial primary production may have been of more value to aquatic than terrestrial consumers and may not have provided much basis for increases in secondary production among the latter.

Evolutionary Aspects

If innovations among continental plants for resource acquisition and for maintenance were the keys to the development of continental ecosystems, what factors controlled *their* evolution? Further, what specific conditions or events determined the mode and timing of their appearance?

I suggested above that the severe resource shortages and the intense physical disturbance characteristic of early continental habitats placed particular emphasis on adaptations for resource conservation and/or for replacement (reproduction and recolonization) relative to those for resource acquisition and resistance to disturbance. In modern resource-poor situations, organisms typically conserve whatever resources are available through very slow growth with very limited investments in (1) resource acquisition, for example, in growth of collecting systems for light, nutrients, and water; (2) resistance to disturbance; and (3) reproduction (Grime, 1977, and 1979, 33–36). This conforms to the classical concept of a "K strategy," of which the lichen consortium seems to be the ultimate example — adaptation to extreme resource shortages (Grime, 1979, 36). In contrast, where circumstances demand high replacement rates, reproductive capacity tends to be emphasized over resource acquisition or resistance to disturbance. The result is dominance by classical "r strategists," forms marked by small size, rapid growth, short lives, simple structure, and capacity for wide dispersal (Grime, 1977, and 1979, 39–45). Many soil and freshwater microphytes represent an extreme version of this adaptive pattern. In intermediate situations, intermediate characteristics appear, basically such that resource conservation mechanisms are imposed on (and limit) replacement capacity. Grime (1979, 65–66) argues that some mosses and liverworts are exemplars of this pattern, near the extremes both of resource limitations and of disturbance. The ecologic distribution of modern tracheophytes suggests that, even with their homeostatic adaptations for resource acquisition and maintenance, they are unable to tolerate extremely low resource levels or very severe disturbance; habitats marked by these features, or by combinations of them, are left largely to lichens and microphytic algae.

This situation implies that the predominant selective forces operating in such extreme habitats oppose adaptations that would require a high initial investment of resources and, by extension, that such "counterselections" in early continental habitats probably opposed evolution of the adaptations for resource acquisition and for regulation of disturbance that characterize most continental macrophytes. Thus the generation and survival of continental macrophyte lineages becomes relatively unlikely and their establishment a rather improbable kind of event, one that was, at best, only weakly predictable (or determined) from the ecological setting because of counterselection. The hypothesis that counterselection limited the growth of lineages would be falsified if (1) adaptive patterns in early macrophytes were dominantly for resource acquisition rather than for conservation and/or reproduction; (2) several phylogenetically distinct groups of macrophytes originated independently during the same short time interval; (3) macrophytes originated in resource-poor and/or intensely disturbed habitats; or (4) the pattern of macrophyte evolution was generally the same after establishment of those homeostatic adaptations that increased access to resources and ameliorated environmental disturbance as it was before. All four predictions can be tested on the basis of fossil evidence. If the hypothesis survives such tests, it then provides a base-level, null hypothesis with which to evaluate other scenarios for macrophyte evolution.

The hypothesis appears to pass the first test although characterization of adaptive patterns in earliest continental macrophytes must be somewhat tentative. Of the earliest occurrences, the small, thick-walled spores suggest an adaptation for survival and dispersal in severely disturbed circumstances (Grime, 1979, 115). The cuticlelike sheets of cells suggest adaptation for conservation of water in the face of severe desiccation. Certainly, the very restricted development of both aerial and subterranean components in Silurian and even early Devonian tracheophytes is consistent with a resource conservation pattern (Grime, 1977), and the emphasis among early tracheophytes on vegetative reproduction (Tiffney, 1981; Tiffney and Knoll, in press) is also compatible with survival in resource-poor situations (Grime, 1979, 113–14). Even the erect form may be as related to spore dispersal (Tiffney, 1981) as to the acquisition of light. This is not to argue that the features are entirely the consequence of adaptations for resource conservation. The lack of roots might be due to the temporary lack of a developmental solution to the problem of anchorage and of nutrient and water uptake; the occurrence of prostrate rhizomes might be the result of structural weaknesses in shoot tissues, rather than primarily adaptive to other functions incidental to an obligate prostrate form. Rather, none of these features indicate extensive investment in resource acquisition and therefore do not falsify the hypothesis. Only the vascular system and the stomates can arguably be related to increased acquisition of resources and increased photosynthetic activity. The nematophytes are less well understood than the tracheophytes, but what is known suggests an adaptive pattern comparable to that of tracheophytes, since nematophytes lack stomates for carbon dioxide intake and have yet to yield any definite traces of a rhizome-rhizoid system.

On the other hand, the rough coincidence in time of appearance of nematophytes and tracheophytes (within 20 million years or less) appears to negate the hypothesis. If the events were truly independent and could have occurred randomly at any time after the appearance of continental eukaryotric algae, perhaps 800 million years ago, their occurrence by chance in the same 20-million-year interval would seem to be very small. However, the critical assumptions in this argument are that the events are "truly independent" and that they could have occurred "randomly at any time." The former assumption almost certainly does not hold, even if nematophytes and tracheophytes had completely separate origins from terrestrial or aquatic microphytes. The appearance of either group, even in prototypic form, would likely have increased local resource levels and/or moderated disturbance, thereby creating richer and less hostile habitats in which the intensity of counterselection would have been relaxed and the likelihood of homeostatic adaptations increased. In effect, the evolution of one group could have induced the origin of others.

The second condition, temporal randomness, is also unlikely. Certainly, geographic and climatic fluctuations through the late Proterozoic and early Paleozoic must have produced major changes in the number of habitats favorable for macrophyte evolution and thus induced some degree of temporal determinism. Therefore the null deduction must be restated: the counterselection hypothesis is incorrect (as stated) if the number of relatively rich, undisturbed habitats was exceptionally small from the late Ordovician through the early Silurian. Here the evidence — and interpretations of it — are quite ambiguous. Pratt, Phillips, and Dennison (1978) argue that continental macrophytes arose from preexisting marine macrophytes when the latter were exposed to increased disturbance (and presumably decreased resources) during low stands of sea level in the late Ordovician and early Silurian. Gray and Boucot (1978; also Boucot and Gray, 1982) deny such an association; they point out that changes in sea level would have been sufficiently slow to permit migration of marine populations as the geographic distribution of neritic habitats changed. I add that there is no strong evidence that either nematophytes or tracheophytes originated from marine macrophytes (Stebbins and Hill, 1980) or that fluctuating sea level would produce a decrease (or increase) in the number of habitats favorable for evolution of either lineage from aquatic or terrestrial microphytes. Gray and Boucot (1977) suggest a similar linkage to the appearance of monsoonal climatic regimes in the Silurian and Devonian. The mechanism would again be intensified selection associated with seasonal desiccation of alluviodeltaic environments; however, as Gray and Boucot observe, this would require that pre-Silurian climates lacked monsoonal or other wet/dry regimes — a condition for which no evidence is available at this moment. Overall, the counterselection hypothesis is not falsified by evidence now available on the abundance of favorable habitats in the critical Ordovician-Silurian interval — but then, neither is it supported.

The third potential test, the character of specific habitats in which macrophytes originated, also seems to be met by the counterselection hypothesis, so far as interpretation of those habitats can be pushed. The early macrophyte occurrences represent either lowland aquatic or riparian alluviodeltaic habitats (or assemblages transported from such situations into adjacent, near-shore marine environments); these are situations that would have been relatively rich in resources and little disturbed. In addition, the spore assemblages from these rocks give no evidence for any floral sources beyond the recorded lower coastal plain assemblages (K. C. Allen, 1981). Finally, even as late as the middle and late Devonian, tracheophyte remains are very rare or totally absent in "upper" alluvial plain deposits and even in nonriparian lowland sites. Again, such evidence does not "prove" the hypothesis but is at least consistent with it.

The results of the fourth test, the patterns of evolution before and after establishment of macrophyte-level maintenance and resource access, also conform to the hypothesis rather than falsify it. A radical change in macrophyte evolution does occur from the late Silurian onward. The evolutionary mode appears more strongly determined, more predictable, and primarily for features that augment or complement resource acquisition and, for the first time, resource preemption; they also show far less emphasis on reproductive capacity and more on maintenance. Thus in 30 million years or less, most of the principle macrophyte adaptive types were well established. Increased capacity for maintenance and resource acquisition reduced counterselective pressures for small size, limited growth, and simple structure, and reinforced selection for more efficient maintenance and resource acquisition.

Although a nondeterministic hypothesis for the *timing* of macrophyte evolution cannot be falsified on present evidence, that hypothesis (or any nondeterministic one) provides a parsimonious baseline (null hypothesis) for evaluation of deterministic alternatives. Such an alternative must not only withstand falsification but must be preferable in some other way to a nondeterministic one. In particular it must explain features of the record not otherwise accounted for or, at least, be demonstrably necessary as well as sufficient to explain the timing as well as the pattern of macrophyte evolution. These are quite restrictive conditions, but they seem essential if one is to reduce the "just-so" elements in explanation of historical phenomena. These criteria leave us, in my judgement, without a "favored hypothesis" to explain the timing of macrophyte evolution in continental communities.

Conclusions

Early development of continental ecosystems seems related primarily to a handful of adaptations critical to early macrophyte evolution. These initially involved establishment of effective mechanisms for survival of physical disturbance and for conservation of essential resources. These events most likely occurred in relatively rich and undisturbed habitats where sufficient time and resources were available to support such relatively costly maintenance devices. They were followed by the appearance of features that increased acquisition, utilization, and ultimately preemption of resources, such as taller axes, foliage, and roots. In sum, these adaptations resulted in an increase in primary production and a moderation of disturbance in continental habitats. The ecosystem response, in evolutionary time, was an increase in secondary production and an elaboration of trophic structure marked by increased differentiation, specialization, and diversification at the third and fourth trophic levels. Ecosystem changes began first in habitats in which resources were readily available and disturbance relatively low (that is, in brackish habitats) and proceeded more slowly in freshwater habitats, where resources were less readily available and disturbance more intense, and still more slowly in terrestrial habitats. The pattern of change suggests that resource availability may have been the constraining factor for most aquatic ecosystems and physical stress the constraint for most terrestrial ones.

The early phases of macrophyte evolution were, at the most, weakly predictable because of strong counterselection against energetically expensive adaptations in characteristically resource-poor, intensely disturbed continental habitats. However, accumulation of such adaptations in some of those relatively rare habitats where conditions were more favorable switched the later phase of macrophyte evolution to a strongly predictable one dominated by resource acquisition as counterselection for resource conservation and/or mortality replacement relaxed. Neither evidence nor theory support a converse hypothesis. This model provides a sufficient hypothesis for the pattern of early macrophyte evolution and, since it involves a high level of indeterminacy, provides a basic "null hypothesis" for interpreting those events. Any alternative hypothesis must be shown to be not only sufficient but necessary if it is to be favored over such a null one; such necessity remains to be demonstrated.

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